PENAEID PRAWN RECRUITMENT: GEOGRAPHIC COMPARISON OF RECRUITMENT PATTERNS WITHIN THE INDO-WEST PACIFIC REGION

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Staples, D.J. 1991 09 01: Penaeid prawn recruitment: geographic comparison of recruitment patterns within the Indo-West Pacific region. *Memoirs of the Queensland Museum* 31: 337–348. Brisbane. ISSN 0079-8835.

Despite many years of study, the basic seasonal dynamics and life-history parameters, such as longevity and generation time, still remain poorly understood for many penaeid prawns. Even in the better known commercially important species, considerable controversy still exists as to whether the generation time is one year or six months. This confusion appears to arise mainly from the extreme variability seen both between species and within species in the seasonal dynamics of migrations, growth and abundance which underlies the seasonal cycles of spawning and recruitment at the population level. These in turn have been modified, in many cases, by the impact of fishing, making comparisons of natural cycles extremely difficult. In an attempt to understand this variability, trends in the timing of the main life history events were related to factors which change with increasing latitude (and depth). An equatorial pattern of two generations per year provides the basis for the description of many of the variants seen throughout each species range. Farther from the equator, one or other of the generations tends to dominate, resulting in what is essentially a one year generation time. In more temperate waters, most penaeids become strictly annual with one spawning period and one recruitment period each year. A study of these changes with latitude in *Penaeus merguiensis* is used as an example to demonstrate these latitudinal differences. □ *Penaeids, recruitment, life history, Indo-West Pacific.*

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The world's yield of penaeid prawns is now in excess of 700,000 tons (Garcia, 1988) and forms one of the world's most valuable fisheries. Despite this important position, the outlook for the fishery as a whole is not good. The high price of prawns on the export market during the 1970s and 1980s has stimulated rapid development with inadequate controls. This has lead to excessive fishing effort, over capitalisation, excessive production costs and in some cases depleted stocks. Because many of these fisheries operate in developing countries, reliable stock assessments are few but those available have indicated that the stocks are overexploited resulting in less than optimal returns for the effort expended in their capture. Growth overfishing (capture of individuals at size too small to produce the optimal yield) is common and despite earlier assumptions concerning the resilience of prawn stocks to fishing pressure, recruitment overfishing (fishing effort at a level which will depress future spawning stocks and recruitment) has also been detected in several stocks (Penn and Caputi, 1985). Management measures addressing these problems include the limitation of fishing in space and time (area and seasonal closures) and limitation of effort through input controls. Both the detection of overfishing and subsequent remedial action require detailed knowledge of the dynamics of the prawn's life history in terms of the distribution of the different life-history stages in both space and time. This information is not readily available for many of the world's prawn stocks.

The basic life cycle of penaeid prawns appears to be relatively uniform across the family; all shed eggs directly into the water column, pass through a relatively short larval life consisting of three stages (nauplius, protozoea, and mysis), and develop through postlarval, juvenile, subadult and adult stages. In contrast, the spatial and temporal distribution of these stages is extremely variable. Although many of the more commercially important species spawn at sea and spend their postlarval and juvenile stages in estuarine and nearshore coastal waters, there is a broad continuum of cycles ranging from species which are entirely estuarine to those which are entirely marine (Kutkuhn, 1966; Dall *et al.*, 1990). The temporal variability appears to be even greater.

In this paper I will concentrate on the temporal dynamics of penaeid life histories, starting with a detailed examination of one species (*Penaeus merguiensis*) in Australia, moving on to a comparison of life history patterns of other species throughout the world and finally give a brief account of a comparative study on the seasonality of (*P. merguiensis*) across the Indo-West Pacific. In this way, I hope to provide an assessment of the current knowledge of penaeid life histories as well as future research needed in this field.

PENAEUS MERGUIENSIS IN AUSTRALIA

Munro (1975) provided the first detailed account of the life history of *P. merguiensis* in the Gulf of Carpentaria, Australia, based on field sampling of adult prawns in the south eastern Gulf and juveniles in one of the adjacent mangrove estuaries. Because Munro observed spawning and immigration of postlarvae to occur only in spring, he concluded that the cycle was essentially annual. In a more detailed analysis of *P. merguiensis* from a range of locations, Staples (1979) showed that a simple annual cycle as suggested by Munro, could not explain the rather complex geographical differences in the seasonal timing of postlarval and juvenile prawns that occurred in different areas of the Gulf. Four areas in the Gulf, each characterised by its own pattern of seasonality were recognised and it was suggested that these geographical differences could be explained on the basis of semi-annual cycle of spawning, with peaks in spring and autumn. This pattern of spawning was later confirmed by Crocos and Kerr (1983). Geographical differences in the differential survival of these generations in different areas of the Gulf suggested that the life cycle in the north was dominated by the survival through to juveniles of the autumn spawning whereas the life cycle in south was more influenced by the higher survival of the spring generation. A further complicating factor was that juvenile *P. merguiensis* emigrate out of the estuary to offshore waters mainly during periods of rain (Staples and Vance, 1986) and because rainfall is extremely seasonal in the Gulf of Carpentaria (only one wet season each year) only one pulse of prawns recruit each year into offshore waters.

Based on more recent evidence the life history pattern was reviewed by Rothlisberg *et al.* (1985). In the southern Gulf, larvae from the spring spawning period reach the estuaries as postlarvae 2–3 weeks after hatching and spend 2–4 months as juveniles before emigrating offshore during the summer wet season. After approximately 2 months migration offshore, subadult prawns recruit into the offshore fishery (4–7 months old) and form the basis of the autumn fishery. A proportion of these young recruits become sexually mature and spawn giving rise to the autumn larvae. Most of these larvae never reach the estuarine nursery areas (Rothlisberg *et al.*, 1983) and it is the prawns which escape the autumn fishery and survive through to the next spring which provide the spawning stock to repeat the cycle (Fig. 1). In the north the spring component of the cycle is similar but many more larvae produced from the autumn spawning recruit into the estuaries. More recent information on the seasonal distribution of postlarvae in the northern areas, suggests that the strength of the spring generation of postlarvae and juveniles may have been underestimated in previous studies (Vance *et al.*, 1990) but the general conclu-

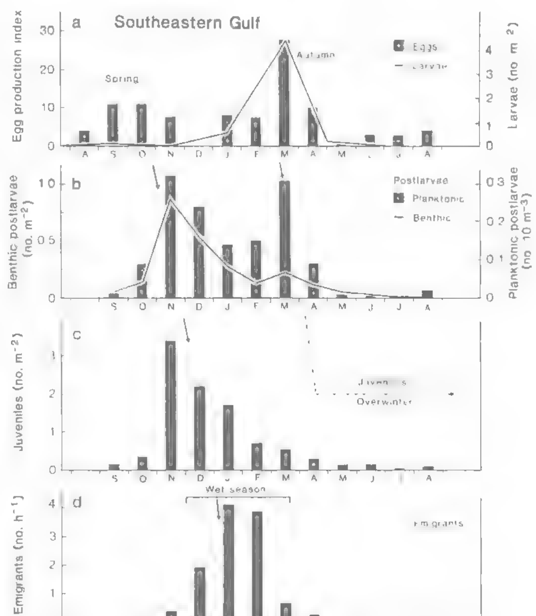

FIG. 1, Seasonal dynamics in the abundance of the main life-history stages of *Penaeus merguiensis* in the southeast Gulf of Carpentaria (from Rothlisberg *et al.*, 1985).

sions have remained unchanged. Because of the unimodal rainfall pattern and offshore recruitment, autumn juveniles contribute less to the offshore fishery than those from the spring generation (Fig. 2).

Rothlisberg *et al.* (1985) suggest that the life history seen in the Gulf was derived from a basic pattern of two equal spring and autumn populations, each contributing to the next generation 6 months later with some survivors of this group contributing again in 12 months, i.e. two interlocking cycles of 6 and 12 months. This implies two wet seasons per year and two periods of offshore recruitment. Another notable feature of *P. merguiensis* in the Gulf is the mismatch between the size of the spawning population and the size of its contribution to the next generation. This is especially apparent in the southern Gulf where the extremely small spring population of females gives rise to the large number of postlarvae and the subsequent offshore fishery. Garcia (1988) has argued that because of the extremely heavy exploitation of *P. merguiensis*, (approximately 80% of the population is caught in the 2 months following recruitment (Lucas *et al.*, 1979), this represents a severe distortion of the basic life cycle, and without fishing the spring spawning would constitute the main reproductive input.

Because the life history of *P. merguiensis* is composed of two interlocking cycles with periods of 6 months and 12 months, there has been some controversy in the literature about the generation time for this species and penaeids in general. At an individual level, generation time is defined as the time between egg and first spawning is 6 months. At the population level, Garcia (1988) argues that the generation time should be defined as the time between the average date of birth of the main generation and the average date of birth of the main group of offspring from the generation. Using this definition, the main generation in the Gulf is obviously the spring generation and the generation time is 12 months.

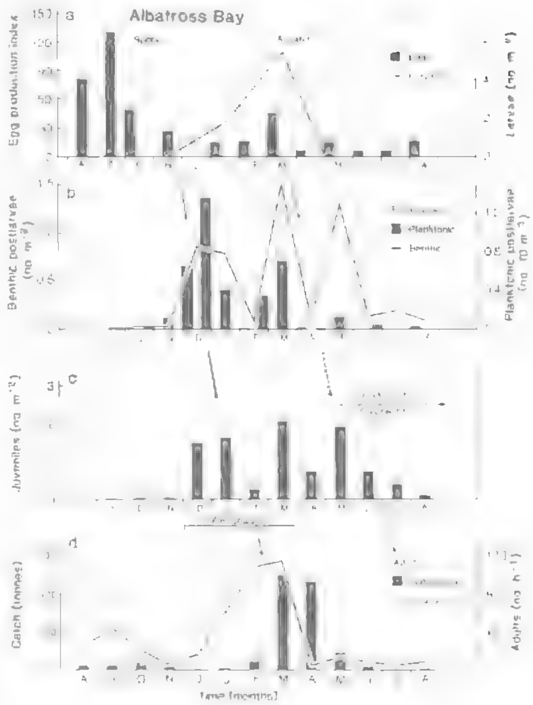

FIG. 2. Seasonal dynamics in the abundance of the main life-history stages of *Penaeus merguiensis* in Albatross Bay, northeast Gulf of Carpentaria (from Rothlisberg *et al.*, 1985).

REVIEW OF WORLD LIFE HISTORY PATTERNS

The life span of most coastal penaeids is between 1 and 2 years in the tropics but is probably longer in temperate waters. The length of time spent in the different life history stages is a function of the growth rate. Environmental factors such as temperature that vary with season, latitude and depth, therefore, also control the time to first maturity, and consequently the generation time. Latitudinal trends reflecting changes in temperature and rainfall patterns, therefore, are extremely important in considering penaeid life history patterns. Similar trends in life-history parameters will also occur with changes in depth. In an attempt to standardise for these effects, I will consider the three latitudinal zones: equatorial (±5°, tropical/subtropical (5–25°) and temperate (>25°), recognising that this is a oversimplification and will not account for areas influenced by local events such as upwellings. However, despite these local events, the classification does assist in the interpretation of observed life-history patterns.

EQUATORIAL PATTERN

Little information is available on penaeids in equatorial regions. However, close to the equator, individual prawns appear to be capable of spawning all year round (Hall, 1962), although seasonal cycles in abundance in prawns will

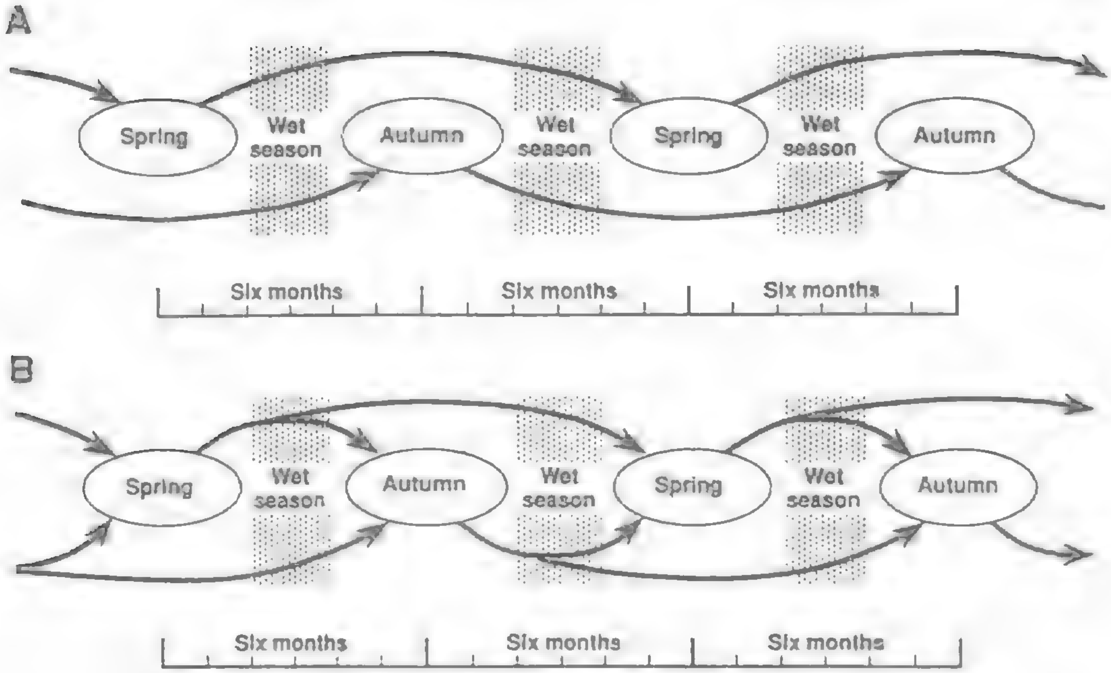

FIG. 3. Schematic life histories of equatorial penaeid prawns. A, alternation of annual generations. B, interlocking six-monthly and yearly generations (from Dall *et al.*, 1990).

result in seasonal spawning activity at the population level (Garcia, 1977). Population cycles are affected by seasonal rainfall, often associated with seasonal monsoons or seasonal temperature changes brought about by the seasonal shifts in the winds, especially in localities close to continental land masses. At the population level, this appears to result in two main periods of increased spawning in each year, even in populations close to the equator (Hall, 1962; Pauly *et al.*, 1984; Staples and Rothlisberg, 1990). These periods of increased spawning tend to occur during the intermonsoonal months of September – November and March – May, periods characterised by decreased winds and currents. By analogy with temperate regions, these periods will be called spring and autumn.

Hall (1962), suggested that this bimodal pattern of spawning was maintained by an alternation of the generations in which the generation time is one year; the spring generation gives rise to the spring generation of the following year and the same for the autumn generation (Fig. 3A). It must be stressed that this interpretation of penaeid life histories is based on an assumption that it took the main species observed, *Metapenaeus moyebi*, one year to reach maturity. We know from the work of Crocos and Kerr (1983) that *Penaeus merguiensis* can mature in 6 months in a sub-tropical area, and a more likely interpretation is that the equatorial penaeids exhibit combinations of 6-monthly and 12-monthly cycles as suggested as a basic scheme for *P. merguiensis* by Rothlisberg *et al.* (1985). This concept has been extended to produce hypothetical scheme for an equatorial pattern which has equal contributions from both the 6-monthly and 12-monthly cycles (Fig. 3B). Obviously more research on equatorial populations is required including more information on the size and age of first maturity and the proportion of the two generations which mature and spawn within their first 6 months of life. The next section of this paper describes a study in the Indo-West Pacific aimed at providing some of this information.

The hypothetical equatorial pattern, although substantiated with few data at this time, does serve as a useful conceptual model for discussing other latitudinal patterns. All of the patterns seen in both the tropical and temperate regions can be derived by the removal or modification of appropriate links.

Tropical/Subtropical Pattern

Bimodal spawning and recruitment are also extremely common in the slightly higher latitudes,

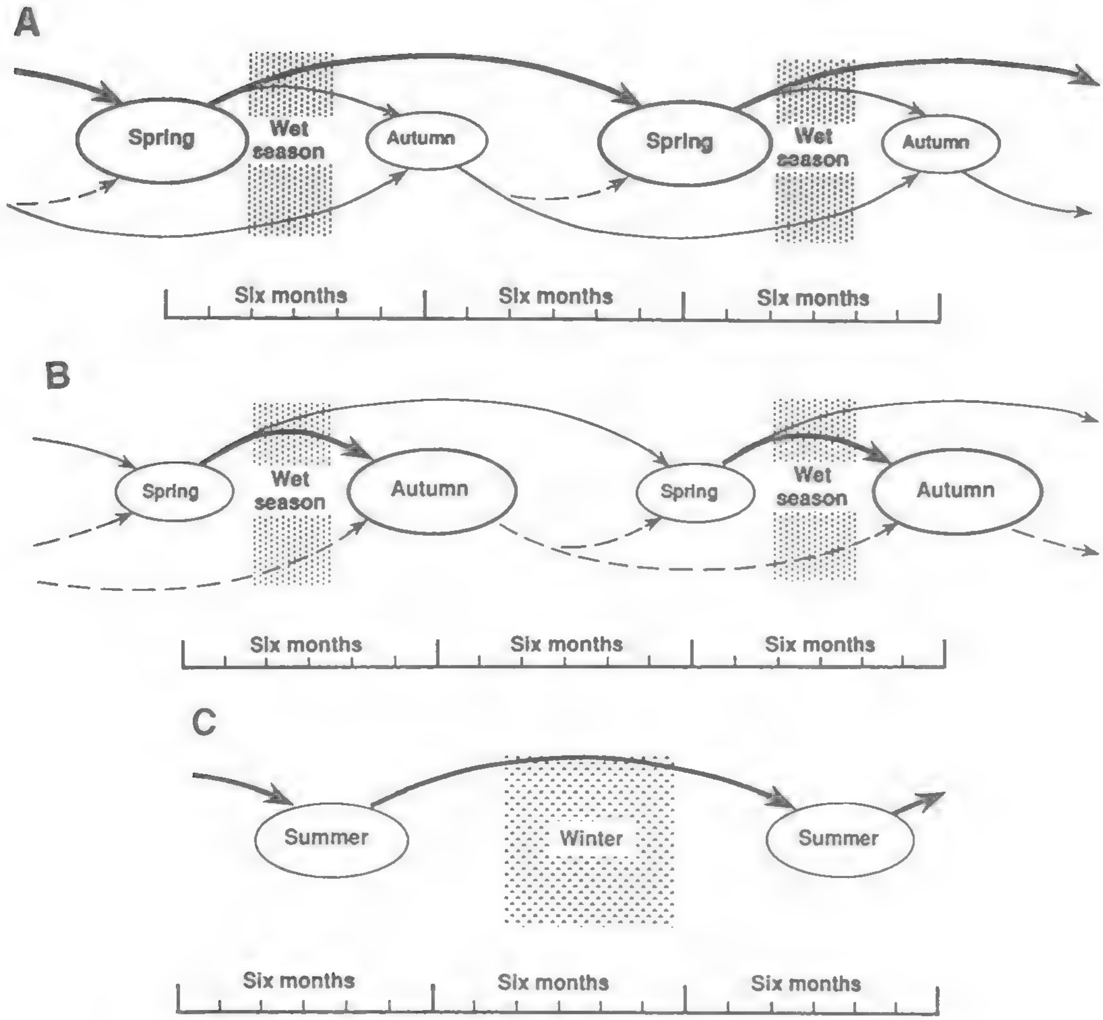

FIG. 4. Schematic life histories of tropical and temperate penaeids. A, 'typical' tropical *Penaeus* pattern (after Garcia, 1985). B, *Penaeus merguiensis* in southeast Gulf of Carpentaria (after Rothlisberg *et al.*, 1985). C, temperate pattern with summer spawning (from Dall *et al.*, 1990).

but in contrast with the equatorial pattern, it appears that seasonal rainfall and lower winter temperature results in either the spring or autumn generation being dominant in the offshore phase. *Penaeus merguiensis* in Gulf of Carpentaria fits into this pattern but is rather extreme in its asymmetry (Fig. 4B). Other examples include *P. notialis* in Senegal (Garcia, 1977; Lhomme and Garcia, 1984), *P. semisulcatus* and *M. affinis* in Kuwait (Mathews *et al.*, 1987), *P. semisulcatus* in northern Australia (Crocos, 1987; Somers, 1987), *P. indicus* in Madagascar (Le Reste, 1971, 1978; Le Reste and Marcille, 1976) and *M. dobsoni*, *P. indicus* and *Parapenaeopsis stylifera* in India (Kurup and Rao, 1975), *P. notialis* and *P. schmitti* in Cuba (Perez *et al.*, 1984a, b). Bimodal postlarval recruitment patterns have been recorded for *P. merguiensis*, *P. japonicus*, *P.semisulcatus* and *P. monodon* in the Philippines (Motoh, 1981) and *P. japonicus* in Natal (Forbes and Benfield, 1986), in Japan (Mito, 1972) and in Korea (Pyen, 1974). Similarly, seasonal postlarval patterns of *M. brevicornis*, *M. dobsoni*, *M. monoceros*, *P. monodon*, *P. semisulcatus*, and *P. indicus* have been reported for several estuaries along the coast of India. A summary of these presented by Babu and Babu (1987) shows that despite considerable local variability, all species show two peaks of increased postlarval abundance within the year in most locations. Bimodal recruitment into offshore fisheries which link to the bimodal pattern of postlarval abundance in India has also been reported by several authors (Kurup and Rao, 1975).

Pérez Farfante (1969), provides a comprehensive summary of the life history of several western Atlantic species. In the tropical/subtropical regions, *P. aztecus*, *P. duorarum* and *P. setiferus* are known to have both spring and autumn generations. This fact has caused considerable confusion in earlier interpretations of Gulf of Mexico prawn life histories. For example, Baxter and Renfro (1967) reported that the postlarval peak in abundance was 6 months out of phase with the peak of larval abundance observed by Temple and Fischer (1967). On the basis of this mismatch, Temple and Fischer suggested that *P. aztecus* must overwinter in the postlarval stage. A more likely interpretation is that one group of workers had observed the spring generation while the other had observed the autumn generation.

Because a life history pattern with disproportionate spring and autumn generations appears to be common in the tropics, Garcia (1985) suggested that this was the typical pattern for the genus *Penaeus* as a whole (Fig. 4A). In this scheme he describes a large spring spawning peak which produces a strong spring generation which recruits into the adult population the following autumn and spawns again the following spring to give a generation time of 1 year for this main generation. A small proportion of the new recruits spawn in autumn giving rise to a small more intermittent autumn generation (Fig. 4A). Garcia, in proposing this model accepted that it may be an over-simplification but that it provided a stimulus for discussion. The literature shows that several *Penaeus* species do not fit the Garcia model. *P. merguiensis* , for example, although having an apparently overall pattern, differs in one important point (compare Fig. 4A and 4B). The proportion of prawns spawning during autumn is much greater and as a result the autumn spawning becomes the major event. Several other studies have also reported that this is the case, including *P. semisulcatus* and *M. affinis* in Kuwait (Mathews *et al.*, 1987), *P. notialis* in north Senegal (Lhomme and Garcia, 1984), *P. notialis* and *P. schmitti* in Cuba (Perez *et al.*, 1984 a, b). Garcia, however, argues that spring phytoplankton blooms are a global occurrence and as a result of increased larval food at this time, natural selection would favour a larger spring spawning biomass. Because all the examples given above are heavily fished stocks, he suggests that in these cases, the spring spawning population may have been severely reduced as a result of fishing the autumn recruits and the populations do not truly reflect the pre-fishing situation. More research on the seasonal dynamics of phytoplankton throughout the tropics would help resolve this debate.

TEMPERATE PATTERN

The influence of temperature on the life history dynamics becomes much more obvious further from the equator. There is a trend for the bimodal spawning pattern seen in many species in the tropics to become unimodal in temperate latitudes. This is usually associated with one well-defined period of recruitment into the offshore fishery each year and the species becomes truly annual with a generation time of 1 year (Fig. 4C). In many species the spawning season shifts to the summer period when temperatures are similar to those experienced during the spring or autumn in more tropical areas of the species distributions. Reported examples of this trend occur in both *P. aztecus* and *P. duorarum* in the western Atlantic. *Penaeus aztecus* spawns both in spring and autumn in Florida Bay, but there is only summer spawning further north along the Carolina coast (Pérez Farfante, 1969). *Penaeus japonicus* is another species with wide geographic range which shows a strong geographical trend in its life history dynamics. Spawning is bimodal over much of its range (as described above) but is confined to the summer months in the Mediterranean (Tom and Lewinsohn, 1983), in Japan (Hudinaga, 1942) and in Korea (Lee and Lee, 1970). In Australia, *P. latisulcatus* has all year-round spawning with two peaks in northern regions, which becomes reduced to a single peak in southern Australia (Penn, 1980). *Penaeus merguiensis*, although exhibiting bimodal spawning over most of its range, is unimodal in the south China Sea with a peak of spawning in spring (Liu, 1986).

Several species with geographical ranges restricted to the temperate zone also have spawning seasons restricted to one period each year. *Penaeus setiferus* shows a unimodal pattern over its entire range. In the Pohai Sea (37°–45°N), *P. chinensis* [= *orientalis*] exhibits an extreme adaptation to a cool temperate climate (Chang Cheng, 1984). Adults spawn in shallow water in early spring at 13°C and juveniles begin leaving the nursery grounds of the Pohai Sea in summer and migrate into deeper waters, where after overwintering offshore they return to the Pohai Sea as mature adults to spawn. In some other cases, prawns spawn in late summer or autumn and it is the juvenile stage which overwinters in the nursery grounds, e.g. *P. plebejus*, Ruello, 1975; *M. macleayi*, Glaister, 1978; *M. bennettae*, Coles and Greenwood, 1983.

As expected, several penaeid species have been shown to have depth related changes in their life history which parallel those seen in changes with latitude. *Penaeus aztecus*, in the Gulf of Mexico, spawns from spring to early winter at 27m depth, with a period of greatest activity from October–December and a smaller peak from March–May. At greater depths, spawning is more or less continuous (Cook and Lindner, 1970).

PENAEUS MERGUIENSIS IN THE INDO-WEST PACIFIC

As seen from the above review several issues require further research. These include:

1. Does the hypothetical life history pattern of interlocking 6-monthly and 12-monthly cycles exist in the equatorial region?
2. Can the life history pattern of penaeids throughout their range be derived from this hypothetical model?
3. In tropical penaeids, is the seasonality of spawning adapted to the seasonality of phytoplankton production where the spring spawning event is the main spawning season as suggested by Garcia (1985)?
4. As a result of 3, is the generation time always one year (defined as the average date of birth of the main generation and the average date of birth of the offspring from this generation)?
5. What other environmental factors are responsible for the variability in life-history patterns seen across a species geographical range?

In an attempt to answer these questions and to provide a better management-orientated research programme for several countries across the Indo-West Pacific region, the Penaeid Recruitment Program (PREP) was established in 1988 under the auspices of the Intergovernmental Oceanographic Commission (IOC) and the United Nations Food and Agriculture Organisation (FAO). By selecting study sites in 6 countries (Philippines, Thailand, Malaysia, Indonesia, Papua New Guinea and Australia) the life history dynamics of *Penaeus merguiensis* can be compared across a range of latitudes, climatic regimes and fishing activities. Additional sites in Brunei, Darussalam and Peoples Republic of China are soon to be included. In all sites, we are attempting to collect data on the seasonal abundance of the major life history stages of *P. merguiensis* and then to compare them across the region.

A full description of the study has been published by Staples and Rothlisberg (1990). Spawning follows a bimodal pattern in most countries (not all countries are able to collect spawning data) during periods roughly coinciding with the temperate spring and autumn seasons. Most data for subadult and adult prawns come from commercial catch sampling and although many other interpretations are possible, it is assumed at this stage that these show seasonal trends in abundance and hence reflect recruitment into the offshore area (Fig. 5). Close to the equator at the Malaysian site the catch per unit effort (CPUE) is high in all months with higher catch rates being recorded from March–May and from September–December (Fig. 5C). Further from the equator at the Indonesian and Thailand sites, recruitment becomes more asymmetrical with the September–December peak dominating. In Papua New Guinea, asymmetry also occurs but the peak is in April–July. At higher latitudes, in the Philippines and Australia, recruitment into the offshore fishery resulted in one major peak in catch rate from October–January in the Philippines and from February–April in Australia.

To date, the programme has demonstrated a clear latitudinal trend from a bimodal recruitment pattern near the equator to an unimodal pattern at higher latitudes. There is also general agreement in the timing of recruitment peaks across the region. Unlike the 'typical' pattern of the genus *Penaeus*, however, the autumn recruitment is not always dominant. An interesting example is that of Indonesia and PNG where although both sites are situated on 8°S, the peaks in recruitment are several months out of phase. Because of the strong correlation between the timing of rainfall and the emigration of juvenile prawns out of the estuary (Staples and Vance, 1986) in Australia, the seasonal timing of rainfall in the six sites was examined to determine whether this factor alone could account for the variability in the pattern of recruitment seen across the region. In general, the seasonal pattern in the CPUE closely followed the seasonal pattern of rainfall in all sites (Figs 5, 6). Australia is the extreme example where the one distinct wet season forces an extremely distinct seasonal pulse in recruitment. In the Indonesian and PNG cases, the phase shift in the recruitment timing also appears to be related to the phase shift in rainfall, with a September–December peak in rainfall in the Indonesian site and a May–July peak in PNG.

In Fig. 7A, the hypothetical equatorial pattern is represented by a bar diagram which joins the two main generations from their time of spawning to their time of recruitment into the offshore region 6 months later. Superimposed on these progressions is a bimodal seasonality of rainfall which coincides with the periods of spawning and subsequent recruitment. Of the 6 PREP study sites, the Malaysian site is the closest representative to the hypothetical equatorial situation. Unfortunately, we do not have spawning data yet, but juveniles and adults appear to closely follow the hypothetical pattern with a bimodal recruitment pattern coinciding with the two wet seasons. In Indonesia and Thailand, a marked asymmetry in both rainfall and recruitment occurs. In both these localities, tracing the two recruitment pulses back to their spawning origins, shows that in both cases the main recruitment event (spring in Indonesia and autumn in Thailand) originated from the smaller of the two spawning peaks (shown as narrow bars in Fig. 7C, E). In Australia and the Philippines, with only one main wet season, one generation is lost almost entirely from the population.

From these preliminary results we can start to answer the questions posed above. It would appear that the different life history patterns seen in *P. merguiensis* across the Indo-West Pacific can be derived from modifications of the hypothetical equatorial scheme. It would also appear that the hypothetical pattern can be found close to the equator in areas experiencing two equal wet seasons each year such as that observed in west Malaysia. More research is needed to establish whether the two generations show a true alternation of generations as suggested by Hall (1962), or whether the pattern is

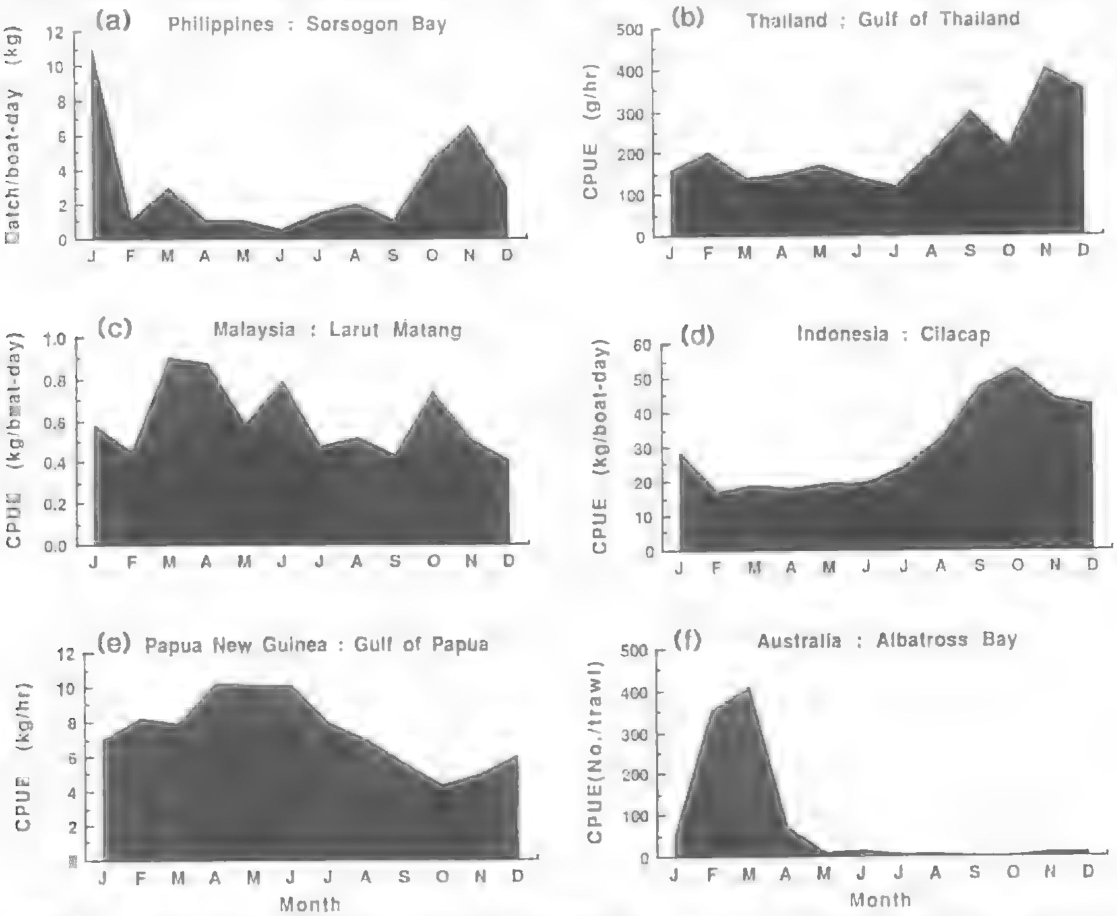

FIG. 5. Seasonal distribution of catch per unit effort (CPUE) of *Penaeus merguiensis* from six localities across the Indo-West Pacific (from Staples and Rothlisberg, 1990).

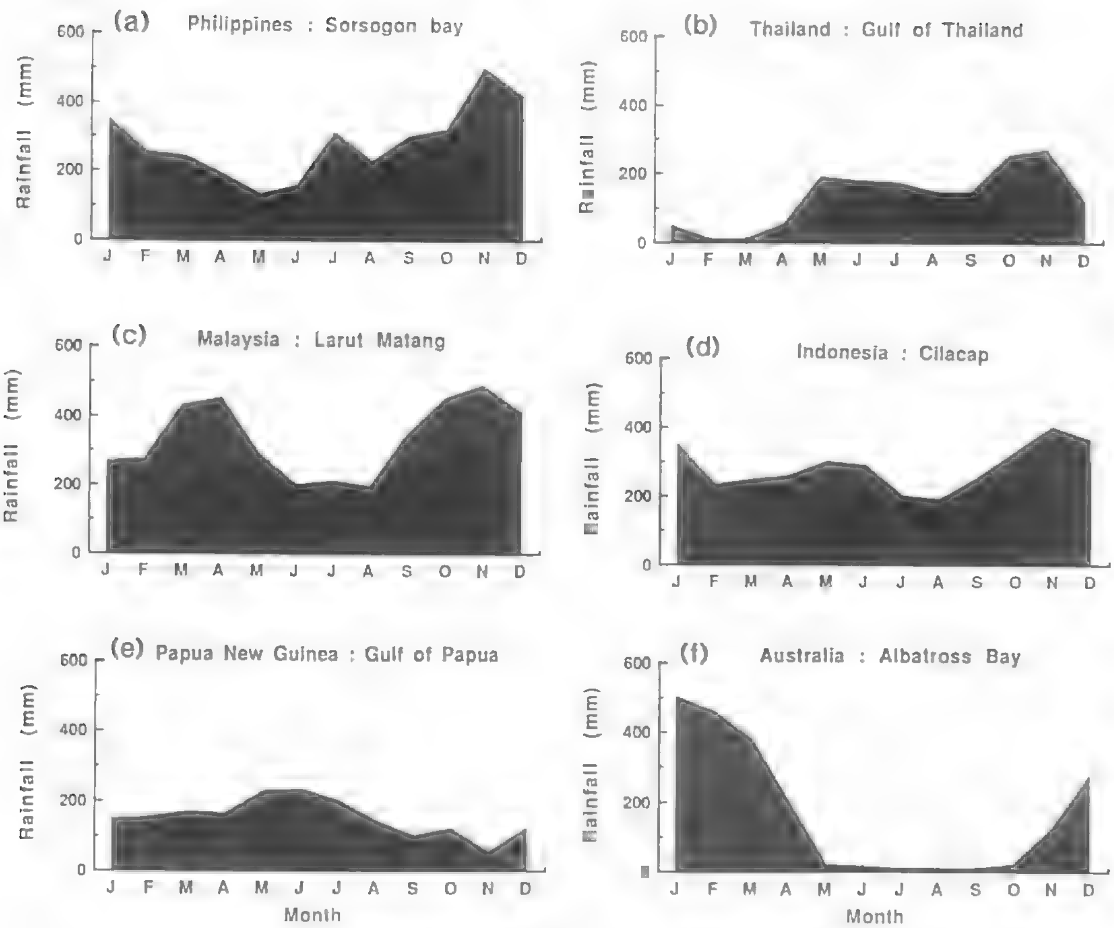

FIG. 6. Seasonal distribution of rainfall at six localities across the Indo-West Pacific (from Staples and Rothlisberg, 1990).

an interlocking of 6-monthly and 12-monthly cycles. Based on the Australian results I suggest that the latter is most likely. Without seasonal phytoplankton results it is also not possible to determine whether the seasonal spawning dynamics is in phase with phytoplankton biomass as suggested by Garcia (1988). However, from the limited data available it does seem likely that the major spawning can occur in either spring or autumn. An obvious reason for the shift is that for *P. merguiensis* the spawning intensity at the population level is greatest at the time of maximum recruitment (large number of small ripe females). This appears to be true in both Thailand and Indonesia, for example, the main spawning season (spring and autumn, respectively) occurs during the time of major recruitment, this event itself being under the influence of rainfall. A testable hypothesis is that the major spawning occurs during or following the major wet season (as a result of major recruitment). This may also link with increased phytoplankton productivity, but not necessarily a spring bloom.

CONCLUSIONS

1. *Penaeus merguiensis* in Australia exhibits a rather unusual life history pattern with two spawning seasons each year, but the main generation of prawns in autumn arising from a rather minor peak of spawning in spring. In some areas of the Gulf of Carpentaria, offspring from the large autumn spawning do not contribute significantly to the subsequent offshore population because of high larval and postlarval mortality.

2. There are many examples of bimodal spawning within the year in tropical penaeids,

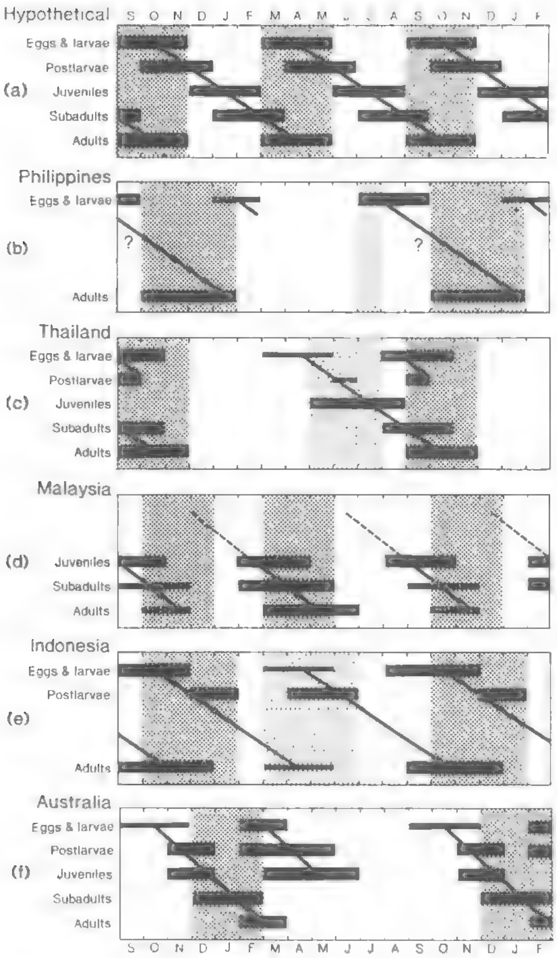

FIG. 7. Seasonal life-history dynamics of *Penaeus merguiensis* as indicated by the cycles of abundance of the main life history stages from five sites across the Indo-west Pacific shown together with a hypothetical equatorial pattern. Light and heavy shaded areas denote minor and major wet seasons (from Staples and Rothlisberg, 1990).

and in many cases a disproportionate survival produces one main and one subsidiary generation (it can be either spring or autumn, but commonly spring). In these cases, description of the generation time is difficult and depends largely on the definition used.

3. It is hypothesised that all these asymmetrical life history patterns are derived from a symmetrical equatorial pattern where both generations interlock in 6-monthly and 12-monthly cycles.

4. In higher latitudes, the bimodal spawning pattern becomes reduced to a single spawning season and the generation time is definitely one year.

5. By comparing the life history dynamics of *P. merguiensis* across the Indo-West Pacific, the derivation of the many variants seen in local life-history patterns can be derived from the hypothetical equatorial scheme.

6. Further research on the factors affecting recruitment strength and timing is needed across a broad geographic range before the basic life history dynamics of penaeids is fully understood.

ACKNOWLEDGEMENTS

This paper represents the work of many scientists. In particular, I thank Peter Rothlisberg and Peter Crocos, CSIRO, Cleveland, Australia for the use of their data to complete the description of the dynamics of *Penaeus merguiensis* in Australia. The collaboration and assistance of scientists in the Philippines, Thailand, Malaysia, Indonesia and Papua New Guinea is also gratefully acknowledged. A large part of the Australian studies were supported by the Fisheries Industry Research and Development Council and the southeast Asian collaborative program was carried out with assistance of grants from the Inter-Governmental Commission of UNESCO (IOC) and the United Nations Food and Agriculture Organisation (FAO).

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